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[Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis.](#)

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1 **Impacts of tropical selective logging on carbon storage and tree**
2 **species richness: a meta-analysis**
3

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16

17 Abstract

18

19 Over 400 million hectares of tropical forest are currently designated as logging concessions. This
20 practice is an important source of timber, but there are concerns about its long-term sustainability
21 and impacts on biodiversity and carbon storage. However, logging impacts vary widely, making
22 generalisation and, consequently, policy implementation, difficult. Recent syntheses of animal
23 biodiversity have indicated that differences in logging intensity – the volume of wood removed ha^{-1}
24 – might help to explain some of these disparities. In addition, it has widely been assumed that
25 reduced impact logging (RIL) might minimise some of the negative effects of logging; though in
26 practice, this has rarely been tested. To test the hypothesis that RIL reduces negative impacts of
27 selective logging once intensity is controlled for, we used meta-analyses of selective logging impact
28 studies, focusing specifically on (1) residual tree damage, (2) aboveground biomass and (3) tree
29 species richness. Our results indicate that RIL appears to reduce residual tree damage when
30 compared to conventional methods. However, changes in aboveground biomass were negatively
31 related to logging intensity. Any effect of RIL, independent of logging intensity, was difficult to
32 discern since it was carried out at relatively low intensities. Tree richness appeared to increase at
33 low intensities but decreased at higher intensities and any effect of RIL was difficult to detect. Our
34 results tentatively support the hypothesis that RIL reduces the negative impacts of logging on tree
35 damage, but do not support suggestions that RIL reduces loss of aboveground biomass or tree
36 species richness. However, this lack of support may be a result of the relative paucity of data on the
37 topic. Based on our results, we suggest that better evidence is needed to assess the differences
38 between the impacts of RIL and conventional logging. Studies that consider plot-level differences in
39 logging intensity are required to fill this knowledge gap. In addition, there must be clarification of
40 whether RIL is an inherently low intensity practice so that this can be factored into management.

41 Introduction

42 Over 400 million hectares of tropical forest are designated as timber concessions, making
43 selective logging – the removal of selected trees from a stand – one of the most widespread human
44 disturbances in tropical forests (Asner et al., 2009). Tropical logging produces approximately one
45 eighth of global timber (Blaser et al., 2011), and is an important contributor to many local and
46 national economies. However, logging can have negative impacts on biodiversity (Berry et al.,
47 2010) and leads to increased carbon emissions (Bryan et al., 2010; Nepstad et al., 1999). Poor
48 management of logging concessions can endanger the long-term sustainability of timber production
49 and there have been suggestions that we might be approaching peak timber production in the tropics
50 (Shearman et al., 2012).

51 Given the large global demand for tropical timber, researchers have proposed modifications
52 to logging techniques to reduce their negative environmental effects, particularly regarding carbon
53 emissions (Putz et al., 2008b) and their impacts on biodiversity (Bicknell et al., 2015). The direct
54 impacts of selective logging are largely the result of the effects of harvesting, skidding of logs, and
55 construction of infrastructure, such as roads, on the mortality and recruitment of trees. The major
56 source of carbon losses is the felling of large trees. However, damage and subsequent death of
57 smaller trees as a result of crushing by felled trees or damage during removal of logs can also be a
58 major contributor of carbon emissions (Putz et al., 2008b). Damage and mortality of non-target
59 trees can also limit forest recovery (Gourlet-Fleury et al., 2013b; Sist et al., 2014) and, if
60 recruitment fails to keep pace with mortality, this can result in altered tree community composition
61 (Ouédraogo et al., 2011). Some of the negative effects of logging on carbon emissions and
62 biodiversity could potentially be minimised by reducing large tree mortality, reducing residual
63 damage to trees that are not felled, or increasing the recruitment of priority species.

64 One of the most widely accepted means of reducing large tree mortality is to limit the
65 minimum diameter at breast height (DBH) at which trees can be cut (Sist et al., 2003a). Placing
66 such limits decreases logging intensity (volume of trees extracted ha^{-1}). In addition to reducing the
67 number of large trees felled, limiting logging intensity can also reduce residual damage to unfelled
68 trees (Mazzei et al., 2010; Picard et al., 2012). In terms of biodiversity, recent work has shown that
69 increases in logging intensity leads to a linear reduction in animal species richness for most
70 vertebrates while a slight increase in bird species richness is observed at low intensities (Burivalova
71 et al., 2014). Similarly, it is likely that species richness of trees might be enhanced at low intensities
72 owing to an influx of shade intolerant species as suggested by the intermediate disturbance
73 hypothesis (Bongers et al., 2009; but see Fox, 2013 for a full discussion of the intermediate
74 disturbance hypothesis).

75 In recent years reduced impact logging (RIL) techniques have been considered to reduce the
76 negative environmental impacts of selective logging (Putz et al., 2008a). Though application of RIL
77 is not uniform, it tends to involve one or more of the following activities: cutting lianas prior to
78 logging, felling trees in predetermined directions to minimise the impact to the surrounding forest,
79 limiting road construction, identification and mapping of trees to be cut prior to logging, and
80 planning of roads and skid trails (Pinard and Putz 1996). Individual studies have suggested that RIL
81 might reduce carbon emissions (Pinard and Putz, 1996), residual tree damage (Sist et al., 2003c),
82 and result in more favourable biodiversity outcomes (Bicknell et al., 2014) when compared to
83 conventional logging. It has also been suggested that RIL could be carried out at similar intensities
84 to conventional logging while causing less damage to residual trees (Pinard and Putz, 1996; Putz et
85 al., 2001; but see Sist et al., 2003). Furthermore, it has been proposed that its wide implementation
86 could reduce global carbon emissions from selective logging by 30% (Putz et al., 2008b). If true,
87 these minimisations in the negative consequences of selective logging could be vital in securing
88 long-term sustainability of timber producing tropical forests.

89 Despite claims made about the benefits of RIL, evidence is conflicting. Studies that
90 investigate the effectiveness of RIL in reducing the negative impacts of conventional logging
91 generally do so by comparing between areas logged using RIL techniques at relatively low
92 intensities. For example, in one of the few studies comparing the effects of RIL and conventional
93 logging on carbon stocks, any treatment effect was confounded by an approximately 50% higher
94 logging intensity in conventionally logged plots (Pinard and Putz, 1996). Moreover, in the studies
95 where differences in the logging intensity have been controlled for, there appears to be little
96 difference in the impacts of RIL on the damage to residual trees (Sist et al., 2003c) and carbon
97 stocks (Griscom et al., 2014). Taken together, these observations bring the value of RIL into
98 question, given that a major aim of RIL is to reduce impact whilst maintaining timber yields (Keller
99 et al., 2003).

100 Though RIL is widely cited as a method for limiting the negative effects of tropical selective
101 logging there is little information regarding its general impact once logging intensities are
102 controlled for. Though Putz et al.(2012) provided a valuable overview of the impacts of tropical
103 selective logging on biomass and tree species richness, no attempt was made to explain differences
104 in these impacts between sites. The recent meta-analysis by Bicknell et al. (2014) indicated that RIL
105 reduced impacts on animal populations, but there are no equivalent syntheses of effects on trees.
106 Given that REDD+ aims to provide economic incentives to reduce loss of carbon and biodiversity
107 from forests (Harvey et al., 2010) and RIL has been suggested as means of attaining these
108 reductions (Putz et al., 2008b), understanding variation in logging impacts is vital to inform
109 management. In this study, we aim to address this knowledge gap by conducting a meta-analysis to

determine which factors relating to logging method and intensity might explain differences in (1) residual stand damage, (2) aboveground biomass loss, and (3) tree species richness.

Methods

Systematic review

We defined selectively logged tropical forests as native forests between the latitudes of 40°N and 40°S subjected to selective tree removal for timber. We undertook a standard systematic review as described by Pullin and Stewart (2006) and used the terms ("biomass" OR "carbon" OR "basal area" OR "damage" OR "snag" OR "non-target" OR "tree" OR "species richness" OR biodiversity) AND (selective logging OR felling OR timber extraction OR reduced-impact logging OR degradation) AND "tropical forest" to search Web of Knowledge, Wiley Blackwell and Science Direct databases. We also used the appendices of Clark and Covey (2012), Gibson et al. (2011), Picard et al. (2012) and Putz et al. (2012) to identify potentially relevant literature. The final literature search was undertaken on 20/06/2014. In addition, we contacted researchers working on the subject to identify any unpublished datasets.

In order to be included in our analysis, studies had to:

- (i) Present data on residual stand damage following logging or aboveground tree biomass and/or species richness of trees from at least one undisturbed forest and one logged forest site.
- (ii) Include sites with spatially replicated measures of tree species richness or aboveground biomass of trees in both logged and unlogged sites with at least three plots present in each. This rule was relaxed for the studies of residual stand damage since very few were replicated or provided comparisons with unlogged sites.
- (iii) Include logged sites that were unaffected by multiple disturbance types such as fire or drought.
- (iv) Be carried out in terrestrial forests, excluding mangroves.

First, articles were excluded if titles were deemed irrelevant. Following this, abstracts were examined to filter out irrelevant articles. The remaining articles were read and retained only if they met the inclusion criteria described above. The search produced 6422 potentially relevant references and, following exclusion of irrelevant papers, we extracted data from 62. If there was evidence that relevant data had been collected but were not presented in the publications, data were requested from authors. If data were presented in tables, they were directly transferred to our database, whereas if data were presented as graphs, we used the program datathief (vIII) (Tummers, 2006) for data extraction. For details of the studies used see Table 1 and Tables S1-S3.

145 In articles that measured changes in biomass or species richness, we extracted the mean,
146 standard deviation, and sample size for sites in logged and unlogged forests. Where multiple sites
147 were measured per study we extracted data for each site separately. In studies of forest damage, we
148 extracted the plot level data of residual tree damage. We also recorded site latitude and longitude,
149 continent on which studies were undertaken, method of logging used (RIL or conventional
150 selective), the number of years since logging, the minimum size of trees measured, and volume of
151 wood extracted ($\text{m}^3 \text{ha}^{-1}$) and/or number of trees felled ha^{-1} . In sites that had been logged twice, we
152 calculated logging intensity as the sum of the volume extracted over both cycles, following
153 Edwards et al. (2013).

154 Sites were defined as RIL if authors used the term to describe the logging methods used. All
155 other sites were classified as conventional. While the definitions of RIL can vary depending on
156 context (Putz et al., 2008a), our comparison between conventional logging and RIL represents real
157 differences in the techniques used at sites. RIL sites tended cut lianas prior to logging more
158 regularly than conventional sites (70.0% vs 10.5% of sites respectively) and the same was true for
159 planning of roads and skidder routes (75.0% vs 5.3%); planned extraction of trees (80.0% vs
160 21.1%); use of directional felling (65.0% vs 5.3%); training of staff to cause lower damage (40% vs
161 0%); supervision of staff during logging (25% vs 0%) and; restriction logging on steep slopes
162 (30.0% vs 2.6%). On average RIL sites employed a mean ($\pm \text{SE}$) of 4.05 (± 0.48) of these techniques
163 that aimed to reduce damage per site, while conventionally logged sites employed 0.47 (± 0.16) per
164 site. These results are summarised in Figure S1.

165

166 **Data preparation**

167 To convert the number of trees harvested ha^{-1} to the metric of logging intensity used in this
168 study (m^3 wood removed ha^{-1}) we produced a linear mixed model, accounting for continent level
169 differences in the relationship between number of trees and volume of wood harvested ha^{-1} .
170 Following this, we used the model to predict the volume of wood harvested ha^{-1} in studies which
171 only provided alternative details of the number of trees removed ha^{-1} , following Bicknell et al.
172 (2014) and Burivalova et al. (2014). We attempted a similar process to convert between different
173 metrics of residual damage following Picard et al. (2012) but found that the number of trees
174 damaged ha^{-1} was a poor predictor of the proportion of residual trees damaged. Therefore only
175 studies that directly supplied information on the proportion of residual trees damaged were used.

176 In order to analyse the impact of logging intensity and logging method on changes in
177 aboveground biomass and species richness, we used a weighted approach. If standard deviations
178 were missing from studies, these were estimated by using imputation methods (Koricheva et al.,
179 2013). To do this, we estimated the relationships between the coefficient of variation for tree

180 richness or biomass and plot size using linear models since smaller sampling plots result in greater
181 between-sample variation (Wagner et al., 2010). We then used linear models to predict the
182 coefficient of variation for studies missing these data, which were subsequently converted to
183 standard deviations to enable weighted analyses. While this is a relatively novel technique, it is
184 likely to bias results less than excluding studies with incomplete information (Nakagawa and
185 Freckleton, 2008).

186

187 **Statistical analysis**

188 To determine the effect of logging intensity and different logging methods on the proportion
189 of residual trees damaged, an unweighted linear mixed model was used. Prior to model fitting, the
190 response variable was logit transformed so that values were constrained between 0 and 1 (Warton
191 and Hui, 2011). Random effects were used to identify data from the same study to avoid problems
192 of non-independence. We tested how logging volume affected the proportion of residual trees
193 damaged and whether logging method changed the slope of this relationship. Previous work by
194 Picard et al. (2012) suggested that the relationship between logging damage and intensity is non-
195 linear, and therefore models with log terms were also tested. The marginal R^2 was obtained using
196 following the method of Nakagawa and Schielzeth (2013) implemented in the R package MuMIn
197 (Barton, 2014). AICc was used to determine the relative likelihood of a model being the most
198 parsimonious. All models of tree damage with a $\Delta AICc < 7$ were averaged to produce coefficient
199 estimates, with models supplying more weight when they had greater support (Burnham et al.,
200 2011).

201 To analyse the effects of logging on carbon pools and tree species richness, the log response
202 ratio of differences between sites was calculated and models weighted so that more precise studies
203 had more weight (Borenstein et al., 2009; Hedges et al., 1999, see Appendix S1). We then fitted a
204 meta-regression model using random effects to account for between study variation that might be
205 due to differences in research methods. In addition, in our analyses of changes in tree species
206 richness, whether species richness estimates were rarefied or not was included as a random effect.
207 We did this because this has been shown to cause between-study differences and was therefore
208 considered an additional source of between-study noise (Cannon et al., 1998; Gotelli and Colwell,
209 2001). Random effects were also included to account for differences in the minimum DBH of trees
210 measured and the time since logging which may have confounding effects on the analysis. Since
211 some studies used the same unlogged site as a comparator for multiple logged sites, we ran
212 bootstrapping routines with 10000 iterations, selecting only one pairwise comparison where the
213 same unlogged site was used as a reference, in order to remove study-level pseudoreplication
214 following Gibson et al., (2011).

215 We tested the effects of logging method (RIL or conventional logging) and logging intensity
216 in determining changes in biomass and tree species richness. The time since a site was logged could
217 also play a role in determining logging impacts (Burivalova et al., 2014) and therefore this was also
218 included in models. After each bootstrapping iteration, models were ranked by AICc and, after
219 bootstrapping, models were ranked according to their median AICc values and the proportion of
220 times the model was considered to be the most parsimonious (Gibson et al., 2011). Parameter values
221 of the model with lowest AICc were calculated by selecting median estimates after 10000
222 bootstrapped iterations. All statistical analyses were performed in R 3.0.2 (R Development Core
223 Team, 2011) with unweighted and weighted analyses carried out using the lme4 package (Bates et
224 al., 2014) and the metafor package (Viechtbauer, 2010), respectively. All figures were drawn using
225 ggplot2 (Wickham, 2009).

226

227 **Results**

228 The systematic review yielded 62 studies, from which we extracted data on residual tree
229 damage from 72 sites, and 43 and 23 paired, replicated sites that measured biomass and tree species
230 richness respectively. In total these data comprised of information on residual damage from 285
231 plots, comparisons of aboveground biomass from 326 logged and 128 unlogged plots and
232 comparisons of tree species richness from 256 different logged and 161 unlogged plots. Median
233 logged-site age for those sites where biomass was measured was 4.5 years and for sites where
234 richness was measured it was 5 years. Sites were mostly located in Asia and the Americas, with
235 relatively few in Africa (Figure 1). Further details of the studies used in our meta-analysis are given
236 in Table 1 and Tables S1-S3.

237 The most parsimonious model for predicting the volume of wood logged ha^{-1} suggested a
238 positive relationship with the number of trees extracted ha^{-1} an interaction between this and
239 continent. The slope of the relationship was steeper in Asia and Africa than in the Americas (Figure
240 2) and overall the model had high explanatory power ($R^2=0.72$).

241

242 **Residual stand damage**

243 The model that best explained the proportion of residual trees that were damaged included
244 an interaction between the logarithm of logging intensity and the logging method ($R^2=0.25$). Only
245 one other model had a $\Delta\text{AICc} < 7$ (Table 2). Model-averaged predictions suggested that residual
246 damage increased as a function of the logarithm of the logging intensity (Slope= 0.54 ± 0.19 ,
247 $P=0.005$, Figure 2, Table S3). This model also suggested that RIL tended to cause less residual
248 damage than conventional logging at the range of intensities studied (coefficient= -1.00 ± 0.37 ,
249 $P=0.007$, Figure 2, Table S4). However, the 95% confidence intervals for predictions were wide

250 indicating large variation in damage to residual tree stems for both methods.

251 252 **Impacts of logging intensity and method on biomass and species richness**

253 Logging intensity was negatively correlated with the response ratio for aboveground
254 biomass following logging (slope= $-0.0042 \pm \text{SE } 0.0008$, $P < 0.001$, Figure 4a, Table S5). This model
255 had good explanatory power (pseudo- $R^2 = 0.43$) and was ranked most parsimonious in all bootstrap
256 iterations (Table 3). Logging intensity was considered the most important variable for predicting
257 post-logging change in biomass as it was present in all models with a $\Delta\text{AICc} \leq 7$ (Table 3).
258 However, it is also clear that there is no model that performs substantially better than all of the
259 others since numerous models had a $\Delta\text{AICc} \leq 7$. In addition the relatively low intensities at which
260 RIL sites tended to be logged compared to conventional sites reduced the power of our analyses to
261 detect differences in impacts between the two methods (Figure 4a).

262 The model that explained variation in tree species richness response ratio most effectively
263 indicated a negative relationship with intensity of logging (slope= $-0.001 \pm \text{SE } 0.0002$, $P < 0.001$),
264 with a positive intercept (Intercept= 0.06 ± 0.01 , $P < 0.001$, Figure 4b, Table 4, Table S6). Only one
265 other model had a $\Delta\text{AICc} < 7$, and the most parsimonious model had a pseudo- R^2 of 0.34. As with
266 aboveground biomass, the relatively low logging intensities used in RIL hindered comparison of the
267 effects of the different methods while accounting for intensity (Figure 4b).

268 269 **Discussion**

270 This study draws on a larger body of evidence than the recent meta-analysis of Putz et al.
271 (2012) on the impacts of selective tropical logging, making it the most precise meta-analysis of the
272 impacts of tropical selective logging on carbon and tree biodiversity to date. In addition, our
273 analyses of the impacts of logging on biomass and species richness accounted for (i) differences in
274 study precision, (ii) study-level pseudoreplication, and (iii) explored the reasons for variation in
275 impacts amongst sites. While the meta-analysis of Putz et al. (2012) was a valuable contribution to
276 the logging literature it did not address any of these issues and as a result the results of our study
277 differ substantially from this previous meta-analysis.

278 Our results indicate that the impacts of selective logging in tropical forests on residual stand
279 damage, biomass loss and species richness change are largely explained by differences in logging
280 intensity. Residual tree damage also appears to be reduced under RIL when compared to
281 conventional logging. However, the effect of RIL on biomass loss was difficult to assess owing to
282 the confounding effects of differences in logging intensity, a problem that is not widely
283 acknowledged in the literature on tropical forest logging. Below we discuss implications of our
284 results and potential solutions to this problem.

285

286 **Impacts of logging on stand damage and biomass**

287 Our meta-analysis indicates that logging intensity is the primary driver of differences in
288 non-target tree damage in selectively logged tropical forests, as noted in previous studies (Johns,
289 1992; Picard et al., 2012; Sist et al., 1998). However, our results from a wide range of sites also
290 support the hypothesis that RIL causes lower damage to residual trees than conventional logging –
291 the first time that such a result has been noted across a large number of different sites. Given that
292 residual damage to trees can account for 20-30% of biomass losses from selective logging as a
293 result of increased mortality from windthrow, disease or fire (Johns, 1992; Mazzei et al., 2010;
294 Panfil and Gullison, 1998), our result indicates that RIL may help to reduce carbon losses at the
295 stand scale. In addition, our results suggest that in order to keep residual stand damage below the
296 25-30% limit that is considered to be sustainable (Huth and Ditzer, 2001; Sist et al., 2003a, 2003b),
297 RIL should be carried out at intensities below $60 \text{ m}^3 \text{ ha}^{-1}$ while conventional logging must be limited
298 to intensities below $40 \text{ m}^3 \text{ ha}^{-1}$ (Figure 3).

299 A large amount of between-study variation was observed in the impacts of logging intensity
300 and methods on stem damage, which suggests that variables we failed to consider may be
301 important, such as the density of log extraction routes or the steepness of slopes where logging was
302 undertaken (Putz et al., 2000). Equally, this variation may be a result of the amongst study
303 differences in methods and metrics used to assess stem damage, as previously noted by Putz et al.
304 (2008a). Our results support Putz et al.'s (2008a) assertion that standardised metrics of logging
305 damage are needed to enable synthesis.

306 Our analyses of the effects of logging on aboveground biomass emphasize that accounting
307 for harvesting intensity is vital. The volume of wood removed ha^{-1} was by far the best predictor of
308 changes in biomass in response to timber harvest. While this point may appear obvious, many
309 studies fail to interpret the effects of logging in the context of the intensity used. For example, the
310 recent meta-analysis by Putz et al., (2012) found that “76% of carbon is retained in once-logged
311 forests,” failing to statistically account for differences in logging intensity. However, results from
312 our study show that this finding of Putz et al., (2012) is only true when forests are logged at an
313 intensity of approximately $50 \text{ m}^3 \text{ ha}^{-1}$ and that there is considerable variation in logging impacts
314 which are driven by logging intensity. Thus, reporting the mean impact of logging on biomass as
315 Putz et al., (2012) did is relatively uninformative.

316 We found little support for the hypothesis that RIL and conventional selective logging
317 differed in their effect on post-logging biomass once logging intensity is accounted for. As such it is
318 impossible to say, from the studies used here, whether RIL causes lower carbon emissions when
319 compared to conventional logging. In part this results from a lack of data from studies of RIL, and

the relatively low logging intensities at which RIL is carried out when compared to conventional selective logging (Figure 5). Keller et al.(2003) argued that RIL is not synonymous with low-yield logging. However, the data used in our study and recommendations by Sist et al. (2003a, 2003c) suggest that part of the prescriptions for RIL may be a reduction in logging intensity. In order to compare the impacts of RIL and conventional logging further clarification is needed on whether RIL is inherently a low intensity practice. Ultimately, timber yields are extremely important for managers of logging concessions and if RIL will always reduce short-term yield this must be explicit. Given the important of yields, even if RIL is essentially a low intensity practice consideration of impacts must account for differences in intensity. Unless studies of RIL are carried out at a similar range of intensities to conventional selective logging its potential benefits, aside from those resulting from lower logging intensities, will remain difficult to assess.

While our study found relatively little evidence for the benefits of RIL for aboveground carbon pools we acknowledge that there is evidence from studies that did not fit our selection criteria that merits consideration. For example, Pereira et al., (2002) found that the size of logging gaps, and thus loss of carbon, was reduced in forests logged using RIL compared to forests logged using conventional methods at similar intensities. In a study that also controlled for logging intensity, West et al. (2014) showed that in a single 24.5 ha plot logged using RIL biomass was reduced by approximately 20% compared to 25% for a plot logged using conventional methods. However, in contrast a recent field study suggested that once logging intensity is controlled for there is little difference between the impacts of RIL and conventional methods on carbon storage (Griscom et al., 2014). There is therefore currently relatively little agreement between field-based studies on the carbon benefits of RIL.

Modelling studies have suggested that over 40-60 years the carbon benefits of RIL may be magnified owing to a reduction in residual damage (Pinard and Cropper, 2000; Putz et al., 2008b). Given that growth of non-target trees is important for carbon sequestration in forests recovering from tropical selective logging (Gourlet-Fleury et al., 2013b), the reduction in residual damage observed in this and other studies points to the potential for RIL to have longer-term carbon benefits that our meta-analysis may not have accounted for. These benefits have been hinted at previously (e.g. Lincoln, 2008; West et al., 2014) but there are currently too few studies to discern whether forests logged using RIL do indeed recover biomass more quickly than conventionally logged forests.

351

Impacts of logging on species richness

As for aboveground biomass, logging intensity best explained differences in tree species richness caused by logging. However, compared to aboveground biomass, the slope of this

relationship was much less steep, with an apparent initial increase in species richness at low intensities. In addition the wide confidence intervals around predictions (Figure 4b) indicate the widespread variation in impacts. The most plausible explanation for a post-logging increase in richness is an influx of generalist species from surrounding non-forest areas (Carreño-Rocabado et al., 2012) leading to an initial post-harvest increase, in-line with previous observations supporting the general pattern of the intermediate disturbance hypothesis (Bongers et al., 2009; Connell, 1978). Similar relationships have recently been observed between logging intensity and bird species richness, while other vertebrates showed a decline even at low intensities (Burivalova et al., 2014).

Our results suggest that tree species richness may be relatively insensitive to subtle changes in forest cover, as has been noted previously (Cannon et al., 1998). However, changes in species richness provide no information about the identity and function of individual species. Community composition is likely to be impacted by selective logging, with forest-dependent species sensitive to disturbance becoming less abundant or locally extinct (Sheil et al., 1999) and generalist species increasing in abundance (Baraloto et al., 2012; Gourlet-Fleury et al., 2013). However, analysis of logging impacts on community composition is hindered by the fact that most studies of logging are spatially pseudo-replicated, leading to biased estimates of change (Ramage et al., 2013). Despite this pseudo-replication investigation of the functional traits that determine species' presence and abundance in logged forests could prove a fruitful line of research, as has recently been done with bird species (Newbold et al., 2013).

Improving assessments of logging intensity and damage

Our analyses support conclusions by others (Bicknell et al., 2014; Burivalova et al., 2014) that consideration of logging intensity is vital to understand the impact of logging on biodiversity and aboveground biomass. While this is a seemingly obvious point, many studies interpret logging impacts without reference to logging intensity. One reason for this is that it can be difficult to obtain statistics on the volume of wood removed from an area, and when such data are available they are often only available as a mean volume removed ha^{-1} for the entire study area. For individual studies, identification of the importance of logging intensity is extremely difficult. To solve this, the use of metrics of logging intensity such as basal area logged ha^{-1} may prove fruitful (Mazzei et al., 2010). This has the advantage of allowing an estimate of logging intensity at the plot scale, allowing for more nuanced analyses of logging impacts than is currently possible for most studies. Connected to this point, though we are confident that the methods used in RIL and conventional sites differed, detailed descriptions of the methods used for logging were rare. Where possible studies should report in detail on the logging methods used to allow for easier comparison between studies.

A wide variety of different measures are used to assess residual logging damage in

selectively logged forest stands (Picard et al. 2012), fostered by different objectives and hypotheses. We attempted to convert between different measures to maximise the value of available data, but found that this was not possible due to the poor descriptive value of models. Future syntheses would be aided by standardisation of metrics. As Putz et al. (2008a) and Picard et al., (2012) previously recommended, we support the use of standardised metrics that assess tree damage at the level of individual trees. We also suggest that future studies should report the proportion of basal area that is damaged to provide additional information of logging impacts on forest biomass. Furthermore, stratification of logging damage by tree size class would allow an assessment of its potential demographic effects and would therefore aid our understanding of the recovery of logged forests.

Reducing the negative effects of logging

The results of our study and those of Burivalova et al. (2014) suggest that logging intensity drives carbon and species loss while Becknell et al. (2014) suggest that RIL is less damaging for animal populations. As such, current evidence suggests that RIL at relatively low intensities is likely to be the best way to reduce carbon and biodiversity loss in tropical logged forests. However, given the massive area of tropical forest already designated for logging (Asner et al., 2009), reductions in local intensity, and therefore timber yield, may encourage expansion into previously unlogged areas. This mirrors the situation in agricultural landscapes where the biodiversity benefits of high-yield farming in small areas as opposed to low-yield, extensive farming is debated (Phalan et al., 2011; Rey Benayas et al., 2012). The land-sparing/sharing framework is becoming more prevalent in the logging literature (Griscom and Goodman, 2015), and the only empirical study of this to date suggests that high intensity logging over a smaller area ('land sparing') has better outcomes for tropical forest species than low-intensity extensive timber extraction ('land sharing') in Borneo (Edwards et al., 2014). We hope that the recognition of the importance of timber yields in this context will encourage a more realistic debate about the value of different logging methods and how to balance yields and environmental priorities.

Although reductions in logging intensity may reduce impact, the high demand for timber requires solutions that do not drastically reduce current yields but reduce impacts on forest ecosystems. Methods such as thinning to remove non-timber tree species appear to aid recovery of floral community composition (Ouédraogo et al., 2011), carbon (Gourlet-Fleury et al., 2013b) and timber stocks (Peña-Claros et al., 2008a), and if used in conjunction with other techniques may improve the sustainability of selective logging. When silvicultural treatments are implemented their impacts on different species will need careful consideration so that the growth and recruitment of priority species can be maximised (Peña-Claros et al., 2008b). RIL, along with other measures such as silvicultural treatments, increasing the length of logging cycles and reductions in logging

intensity, may help to improve the sustainability of tropical timber production (Huth and Ditzer, 2001; Pinard and Cropper, 2000; Sist et al., 2003a). However, further evidence is required to verify the benefits of RIL for aboveground carbon storage and tree biodiversity. One potential solution to this lack of evidence is the use of existing data from collaborative networks such as The Tropical Managed Forests Observatory (Sist et al., 2015) while accounting for between-plot variation in logging intensity. Such analyses would contribute towards more sustainable tropical logging practice by providing a more robust evidence base than is currently available.

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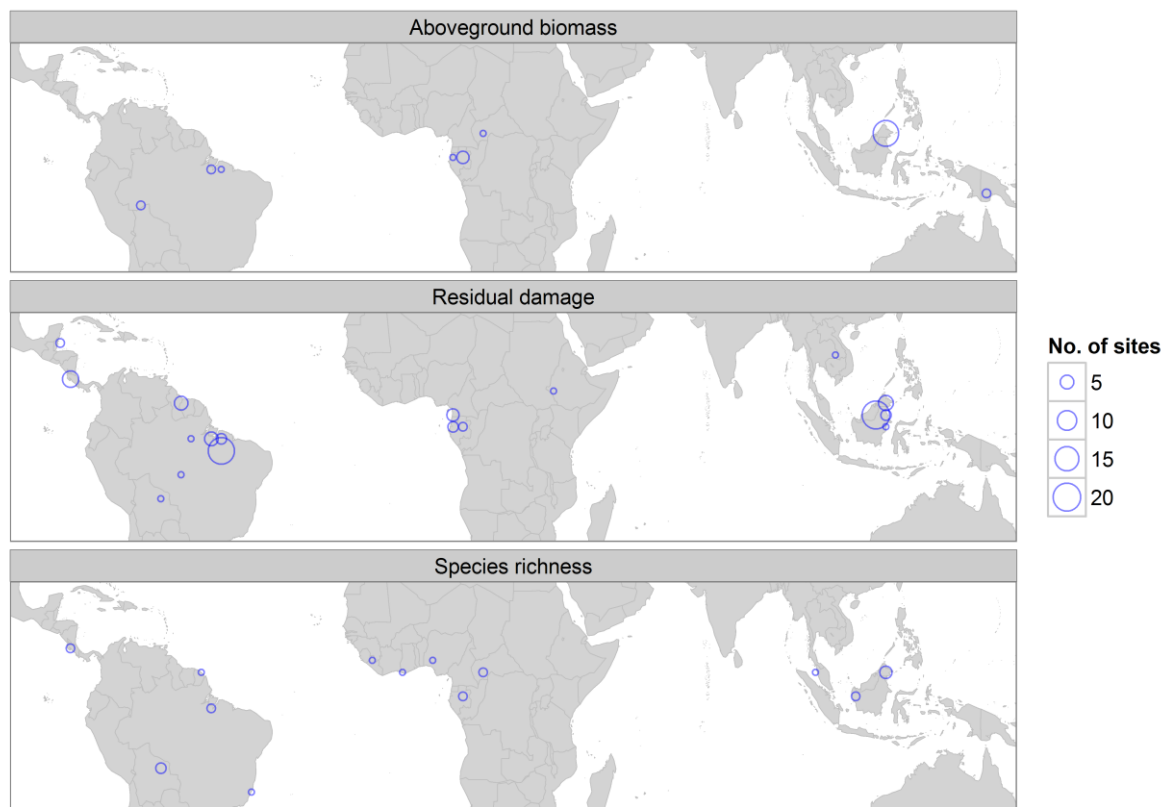
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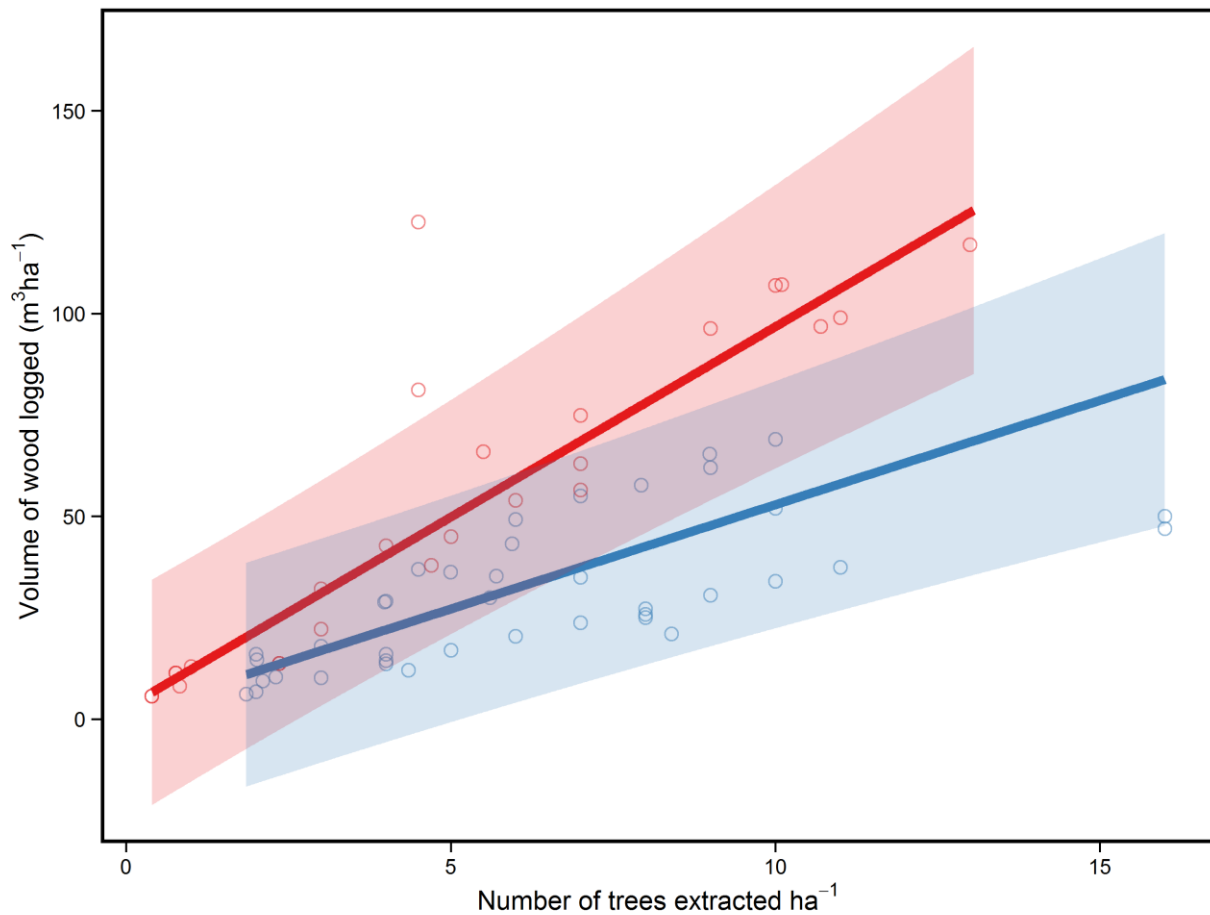
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673 **Figures**
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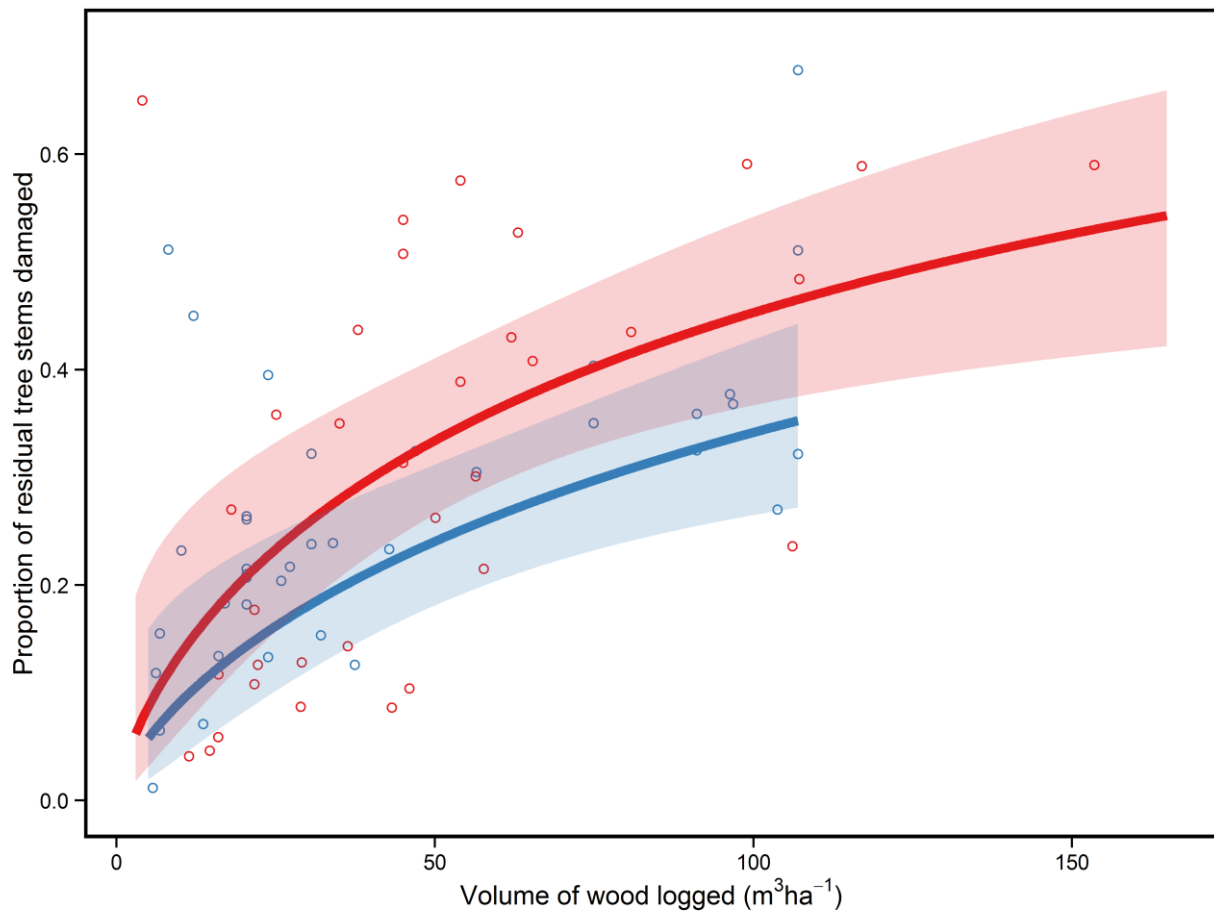
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676 Figure 1 - Geographic location of studies used in our meta-analyses of residual damage,
677 aboveground biomass and species richness responses to selective logging



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679 Figure 2 – The relationship between the number of trees extracted ha⁻¹ and the volume of wood
 680 logged ha⁻¹ for Asia and Africa (red) and the Americas (blue). Points represent individual sites, solid
 681 lines the predictions from the most parsimonious mixed model with bands representing 95%
 682 confidence intervals of the coefficients.

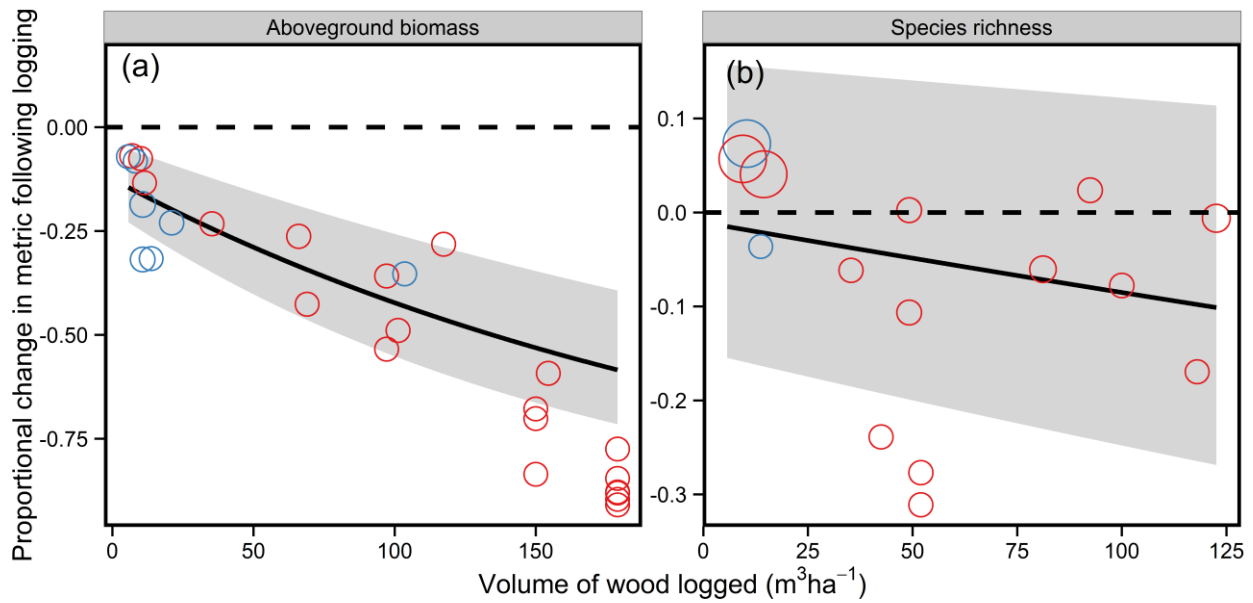
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685 Figure 3 - Impact of selective logging intensity and logging technique on the proportion of residual
 686 tree stems damaged in tropical forests (n=72). Points represent single sites, solid lines are the
 687 predictions the most parsimonious linear mixed effects model ($R^2=0.27$) and shaded areas represent
 688 the 95% confidence intervals of these estimates. Red points and lines refer to sites where
 689 conventional harvest methods were used and blue points and lines where RIL techniques were used.
 690 For details of alternative models considered see Table 2.

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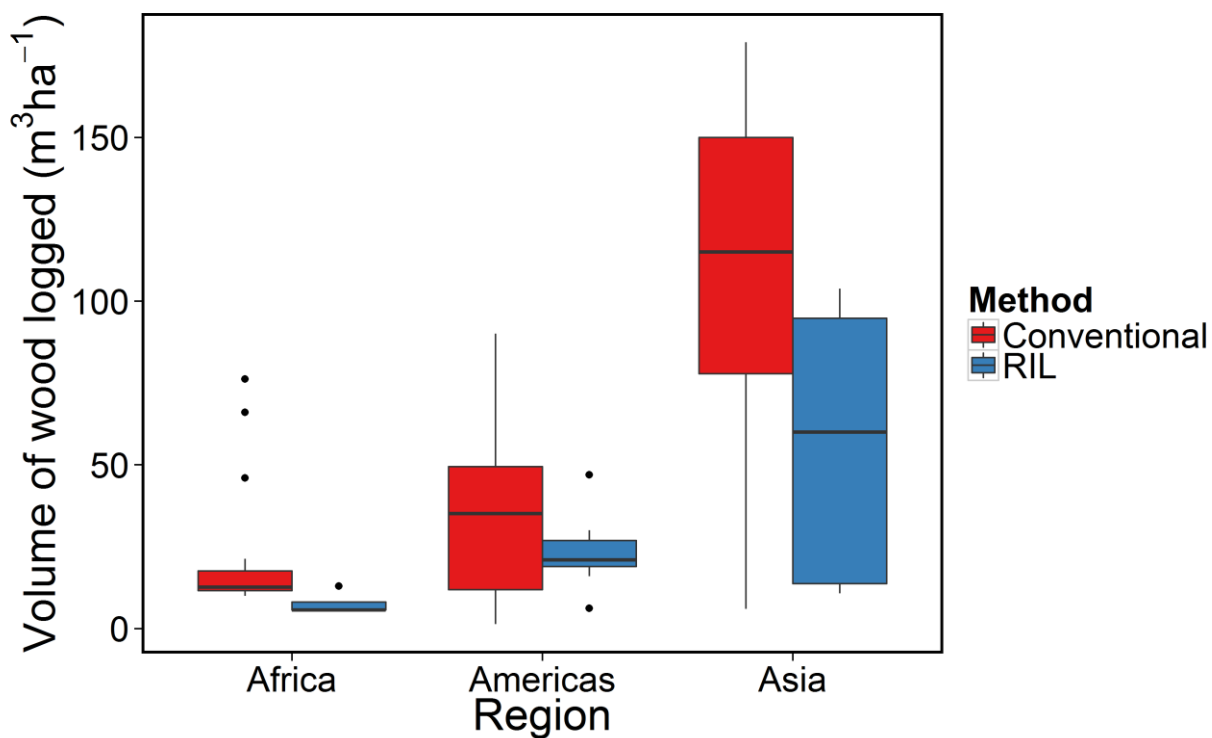


692

693 Figure 4 – Impacts of selective logging intensity on changes in (a) aboveground biomass (n=32) and
 694 (b) tree species richness. Blue symbols are those sites where reduced impact logging (RIL) was
 695 carried out, red symbols correspond to conventionally logged sites with size indicative of study
 696 weight. The solid lines represents the predictions from the weighted meta-regression models with
 697 lowest and shaded area the corresponding 95% confidence intervals. The horizontal dashed line
 698 indicates when there is no difference between logged and unlogged sites. Note that RIL sites tend to
 699 be logged at a lower intensity than conventionally logged sites. Alternative models considered are
 700 detailed in Tables 3 and 4.

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Figure 5 – Variation in logging intensity (measured as volume of wood extracted per hectare) by region and logging method for all studies used in our meta-analyses. Note that conventional logging tends to have higher logging intensity on all continents.

709 **Tables**

710 Table 1 – Details of studies used for analyses of changes in aboveground biomass and tree species richness following selective logging in tropical
 711 forests.

Study	Variable	Response ratio	Effect size variance	Volume logged (m ³ ha ⁻¹)	Time since logging (years)	Method	Continent
Berry et al., 2010	AGB	-0.77	0.06	97.2	0	Conventional	Asia
Bryan et al., 2010	AGB	-0.21	0.01	10.7	1	RIL	Asia
		-0.38	0.01	10.7	1	RIL	Asia
D'Oliveira et al., 2012	AGB	-0.07	0.01	6.9	1	Conventional	Americas
Gerwing, 2002	AGB	-0.26	0.01	35.3	5	Conventional	Americas
		-0.56	0.02	69	5	Conventional	Americas
Gourlet-fleury et al., 2013	AGB	-0.31	0.01	66	0	Conventional	Africa
Imai et al., 2012	AGB	-0.38	0.05	13.74	8	RIL	Asia
Mazzei et al., 2010	AGB	-0.26	0.00	21	0	RIL	Americas
Medjibe et al., 2011	AGB	-0.08	0.01	8.11	0	RIL	Africa
		-0.08	0.01	8.11	0	RIL	Africa
Medjibe et al., 2013	AGB	-0.07	0.05	5.7	0	RIL	Africa
		-0.07	0.05	5.7	0	RIL	Africa
		-0.14	0.04	11.4	0	Conventional	Africa
Pfeifer et al., 2015	AGB	-1.49	0.46	179	10	Conventional	Asia
		-1.81	1.43	150	10	Conventional	Asia
		-1.21	0.46	150	10	Conventional	Asia
		-1.21	0.51	150	10	Conventional	Asia
		-1.87	0.93	179	10	Conventional	Asia
		-1.13	0.40	150	10	Conventional	Asia
		-2.40	2.60	179	10	Conventional	Asia
		-2.13	1.53	179	10	Conventional	Asia
		-2.26	1.99	179	10	Conventional	Asia
		-2.11	1.46	179	10	Conventional	Asia

Table 1 continued

Pinard and Putz, 1996	AGB	-0.90	0.03	154	0	Conventional	Asia
		-0.44	0.02	103	0	RIL	Asia
Rockwell et al., 2014	AGB	-0.08	0.03	10	1	Conventional	Americas
Saner et al., 2012	AGB	-0.33	0.03	117.38	0	Conventional	Asia
Tangki and Chappell, 2008	AGB	-0.67	0.01	101.2	11	Conventional	Asia
Baraloto et al., 2012	Richness	0.0082	0.0032	55	20	Conventional	Americas
Berry et al., 2008	Richness	0.0636	0.0013	92.4	18	Conventional	Asia
Burghouts et al., 1994	Richness	-0.0808	0.0033	100	12	Conventional	Asia
Cannon et al., 1998	Richness	-0.3727	0.0059	52	1	Conventional	Asia
		-0.2730	0.0064	42.5	8	Conventional	Asia
Carreño-Rocabado et al., 2012	Richness	0.0706	0.0001	10.4	0	RIL	Americas
		0.0554	0.0001	9.4	0	Conventional	Americas
		0.0398	0.0001	14.4	0	Conventional	Americas
Foody and Cutler, 2003	Richness	-0.1858	0.0139	118	10	Conventional	Asia
Gerwing, 2002	Richness	-0.0635	0.0052	35.3	5	Conventional	Americas
		-0.3242	0.0044	52	5	Conventional	Americas
Gourlet-Fleury et al., 2013a	Richness	-0.0624	0.0009	81.16	24	Conventional	Africa
		-0.0062	0.0006	122.57	24	Conventional	Africa
Imai et al., 2012	Richness	-0.0370	0.0295	13.74	9	RIL	Asia
Villela et al., 2006	Richness	0.1178	0.0340	90	5	Conventional	Americas
Webb and Peralta, 1998	Richness	0.0024	0.0022	49.2	1	RIL	Americas
		-0.1127	0.0020	49.2	0	RIL	Americas
Cazzolla Gatti et al., 2014	Richness	-0.1575	0.0485	100	15.09615	Conventional	Africa
		-0.7080	0.0372	100	15.09615	Conventional	Africa

713 Table 2 – Rank of different models considered for the description of residual stand damage
 714 following selective logging in tropical forests. Models are ranked by median AICc.
 715

Variables	Degrees of freedom	Log Likelihood	AICc	ΔAIC	AICc weight	Marginal R²
log(Volume) + Method	7	-67.62	150.99	0.00	0.72	0.33
log(Volume)	6	-70.27	153.82	2.83	0.17	0.29
log(Volume)*Method	8	-68.28	154.84	3.85	0.10	0.32
Method	6	-74.15	161.59	10.59	0.00	0.05
Volume+ Method	7	-73.91	163.57	12.58	0.00	0.28
Volume	6	-77.76	168.81	17.82	0.00	0.23
Volume*Method	8	-78.06	174.40	23.40	0.00	0.30
Null model	3	-86.68	179.71	28.72	0.00	0.00

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717

718 Table 3 – Rank of different models considered for description of post-logging changes in
719 aboveground biomass. Models are ranked by their median AICc so that the top model is that which
720 tended to be considered most parsimonious across bootstrap iterations. π_i refers to the proportion of
721 bootstrap iterations in which an individual model was selected as most parsimonious following
722 Gibson et al. (2011).

Model variables	Model rank	π_i	Log likelihood	AICc	Δ AICc	Pseudo- R^2
Volume	1.0	1.00	5.21	0.90	0.00	0.43
Volume*Method+Volume ²	2.0	0.00	8.37	3.66	2.79	0.58
Volume*Method	3.0	0.00	8.34	3.73	2.86	0.58
Voume+Volume ²	4.0	0.00	5.32	4.81	3.63	0.44
Volume*Age	5.0	0.00	6.02	8.36	7.17	0.48
Volume*Age+Volume*Method	6.0	0.00	9.69	14.62	13.18	0.64
Age	7.0	0.00	-2.36	16.05	15.15	0.09
Null	8.0	0.00	-4.33	16.51	15.80	0.00
Method	10.0	0.00	-2.88	17.09	16.27	0.06
Volume*Method+Volume ² *Method	10.0	0.00	8.41	17.19	16.32	0.58

725 Table 4 – Rank of different models considered for description of post-logging changes in tree
 726 species richness. Models are ranked by their median AICc so that the top model is that which tended
 727 to be considered most parsimonious across bootstrap iterations. π_i refers to the proportion of
 728 bootstrap iterations in which an individual model was selected as most parsimonious following
 729 Gibson et al. (2011).

Model variables	Model rank	π_i	Log likelihood	AICc	ΔAICc	Pseudo- R²
Volume	1	0.42	-6.60	5.20	0.00	0.30
Age	2	0.00	-7.88	7.76	2.56	0.19
Method	3	0.34	-9.62	11.24	3.48	0.00
Null	4	0.25	-12.76	17.51	6.28	0.00

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